

XXXIII.—*On the Relationship of the Rodentia to the Marsupialia.* By Dr. A. FLEISCHMANN*.

THE group of the Rodents includes a great number of multifarious forms; generally small and active animals, they are able to adapt themselves to the most different conditions of existence over wide limits, and in consequence of the flexibility of their requirements they people the surface of our planet in astonishing quantity. Their palæontological range extends back to the commencement of the Tertiary period. It is remarkable that even then there were forms living in great numbers which have maintained their full power of existence with but trifling changes to the present day. In the strata which furnish us with the knowledge of those times, however, remains of gigantic Rodents are preserved which flourished side by side with smaller allied forms, but owing to unfavourable conditions soon disappeared again. Now we have along with families of almost universal distribution others whose dwelling-places are limited to particular regions, and the last giant among the Rodents, the *Capybara*, leads a solitary existence in the marshy plains of the South-American rivers.

It might be thought that a group of animals with a history extending so far back in time and showing such remarkable conditions of geographical distribution and so elegant a bodily structure would have induced many naturalists to come forward as its historiographers. But from the study of the literature this expectation appears to be a deceptive one.

It is true that we can cite abundance of works upon the systematic arrangement of this class and the relationship of the different species and families founded upon the structure of the teeth. If we leave out of the account the special researches which have been made upon the typical experiment-animals of our laboratories, the guinea-pig and the rabbit, anatomical investigations upon the constitution of the different systems of organs have been, since the time of Pallas, very rarely extended to the whole group. And if the knowledge of the soft parts must be characterized as quite unsatisfactory, the want of works on the phylogenetic history of these animals is still more to be regretted.

Leaving out of consideration the various attempts to refer the Rodents to a certain place in the system, we have here to

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cite only a work of M. Schlosser's 'On the Rodents of the European Tertiary, with Considerations upon the Organization and Developmental History of the Rodents in general' ('Palæontographica,' Bd. xxxi.). Schlosser is the first and only naturalist who, from the standpoint of the modern theory of evolution, has submitted the palæontological remains of the animals in question to a remarkably thoroughgoing treatment, and then made an attempt at a phylogenetic arrangement under close consideration of the skeletal and dental structure of the recent forms. Deductions from very numerous facts led him to the hypothesis that the Rodentia are directly related to the Marsupials. From my own investigations I regard this conception as quite irrefutable; but unfortunately Schlosser was led, half a year after the publication of his exemplary work, to recall his fine demonstrations and even to characterize them as untenable.

Since that time the question has rested completely, for, owing to the little sympathy that many zoologists have with palæontological results, Schlosser's work appears to have become known only to a few.

By some investigations in developmental history I was led several years ago to give more attention to the question of the genealogical relationships existing between the different classes of Mammalia, and I now venture to put forward a brief report upon the results at which I have arrived with respect to the Rodentia.

As the relationship of the Mammalia is determined customarily by the nature and number of the teeth, I will commence my statement with the dentition of the Rodents. The remarkable parallel in dentition between Marsupialia and Rodentia has already been repeatedly dwelt upon without any careful inquiry whether we have here a mere analogy or an actual homology indicative of direct relationship. The course of conversion, according to my observations, which agree well with previous statements, may be traced from the kangaroo-like Marsupials to the true Rodents, the analogous lateral branches of *Phalangista* and *Phascalomys* furnishing opportune evidence of the former intermediate forms. The dentition of *Phalangista vulpina* shows in the upper jaw two canines and six incisors, of which the middle ones are the largest, the lateral the smallest. In the lower jaw there are two large chisel-shaped incisors, the alveoli of which extend as far as to the first molar. Behind the two large incisors there are four smaller ones; there are therefore six incisors in the lower jaw, diminishing in size posteriorly, so that the third pair appears only in the form of very diminutive points

which fall out early in life, but the second pair is long retained. In *Hypsiprymnus* two incisors in the lower jaw work against six in the upper, and of the latter the first pair have grown considerably stronger, while the second and third pairs are of inferior size. In *Phalangista* the six incisors stand in an elegant horseshoe-like curve on the margin of the broad premaxillæ; but in *Hypsiprymnus* the snout has become narrower, the premaxillæ being laterally compressed. Then the four smaller incisors curve more towards the middle, in order to function, as opposed to the upper teeth, in tearing off plants. A large series of skulls of *Hypsiprymnus* shows in what different ways this purpose can be attained. But the four teeth are too weak to be retained with advantage in adaptive groups; hence they undergo the same fate as the corresponding teeth in the lower jaw of *Phalangista*. In this way it seems to me that the typical dentition of the Rodents with its two pairs of incisors has been produced. The transformation of the enamelled and root-bearing incisor into the persistently growing gnawing-tooth furnished with an enamel plate on one side only may also be easily traced in the stem of the Marsupialia. In the group of the Lagomorpha the dentition shows conditions which accord well with my speculations. In the upper jaw, behind the gnawing-teeth, the second pair of small incisors is quite pressed towards the median plane; they are also changed and have acquired the power of persistent growth. The gnawing-teeth themselves, in both the upper and the lower jaw, also have very short alveoli and a slight curvature.

Notwithstanding the undoubtedly important part which the dentition plays in rapid systematic diagnosis I do not think that the notion of a direct blood-relationship can be founded with sufficient certainty upon the similarity of the dentition alone. Therefore I will adduce further proofs.

The horizontally inward projection of the angle in the lower jaw of the Marsupials is well known as a very convenient and striking character. If the Rodents be phylogenetically related to the Marsupials this structure must also be still recognizable; and in fact the comparison of many skulls has shown me that the often-described bending of the posterior angle of the mandible in Rodents, which occurs in variable degrees in different sections of the order, is derivable in a direct series from what is found in the Marsupials. I affirm most decidedly that Rodentia and Marsupialia manifest their relationship by the homologous behaviour of the angle of the mandible. In Muridæ, Sciuridæ, and Myoxidæ this peculiarity is particularly clearly marked, although it has

been somewhat changed by the secondary influence of the musculature there inserted; it does not prevail, however, throughout the whole group, and is always absent in the Hystrichidæ, Subungulata, Octodontidæ, Lagostomidæ, and Leporidæ.

This modification, however, may be referred back to conditions within the Marsupial series, for among them many forms have lost a distinct mandibular angle, such as, for example, *Phascolarctos*. Then the lower jaw, if looked at from the side, appears as a band dilated posteriorly into a triangular plate. Nevertheless the contour of the margin and the pits and bony ridges occurring on the outer surface of the end of the jaw betray the previous history of the part by very intelligible tokens. Even in true Marsupials we find evidence of the endeavour to bring the mandibular angle from the inwardly directed horizontal position into a more vertical one and into the same plane as the ascending branch. In Rodents all desirable steps of the retroversion have been retained, in the end giving origin to the great increase of the surface of the posterior extremity of the mandible.

Side by side with this we recognize a reduction of the coronoid process; very strongly developed in the Marsupials, it is retained in all the Rodents which possess an inwardly projecting mandibular angle, but it becomes small until it nearly disappears in Rodents with a broad mandibular plate.

As I conceive the origin of the dentition of the Rodentia to have passed through stages such as the living survivors of the leaping and climbing Marsupials still display in model, the dentition of their ancestors must have gradually lost the omnivorous character and become herbivorous; consequently the direction of movement of the lower jaw must also at the same time have become modified.

In point of fact this transformation may be still recognized from the position and form of the *condylus glenoidalis* in the lower jaw, which passes from the transverse direction general in the omnivorous Marsupials into a position parallel to the sagittal plane; and, in accordance with this, the *cavitas glenoidalis* on the squamose part of the temporal, which in the Marsupials attains no great extension, becomes gradually longer so as to pass on to the jugal arch and become a long groove-like excavation.

The occurrence of the change of food may be further inferred from the constitution of the digestive organs in the Rodentia. I indicate now only the form and structure of the stomach. Whilst in most Rodents this possesses a pretty simple structure and form, it becomes more highly compli-

cated in the Muriform animals. Even in the common domestic mouse the division of the stomach into two halves, of which that on the left has horny epithelium and that on the right glandular mucous membrane, is very striking. In the Hamster these divisions of the stomach are visible externally, and in the field-mice with persistently growing molars, which are the most specialized, we also find the greatest complication in the structure of the stomach, as, indeed, has already been fully described by Retzius.

The Marsupials possess a true cloaca, and their lineal relations, the Rodents, agree with them pretty directly in this respect. For the former possession of such an arrangement is always manifested by the fact that the external orifices of the urogenital apparatus and the anus are placed close together, so that they nearly touch and are surrounded by common sphincters. In a mature embryo of the beaver I found them close together in a common naked and somewhat sunken area.

In Marsupials the two cornua of the uterus open by separate apertures into the vagina; in the Rodents the same condition prevails, and its homological significance is not destroyed by a short fusion of the two cornua in some few Rodents.

The greatest number of teats is attained in the Marsupialia, Rodentia, and Insectivora. Taking into consideration the circumstance that the occurrence of rudimentary teats in other divisions of the Mammalia indicates reduction from a previous more abundant endowment, the numerous teats of the Rodents should indicate the primitive organization of those animals. Moreover, Gegenbaur has shown that the milk-glands of the Rodentia are in perfect homology with those of Marsupials.

The structure of the larynx is directly connected with that of the Marsupials, as already indicated by Mayer in 1829; and R. Owen has long since stated that the brain of the Rodentia agrees with that of the Marsupialia in essential points. Not only the external form, but the internal structure is homologous in both. In common also there are the poverty of convolutions, the want of a well-developed *corpus callosum*, the strong development of the vermiform body in the cerebellum, and the free position of the *corpora quadrigemina*.

On the spinal cord the spinal nerves are arranged as in Marsupials; the lumbar region especially, according to Jhering's investigations, presents the greatest similarity.

But what particularly confirms me in adhering to the assertion that the Rodents are related to the Marsupials in a

direct line consists in the numerous and striking similarities which occur in the two groups during embryonic development. If the yelk-sac of the opossum during its uterine existence is of considerable extent, and at the moment of birth considerably exceeds the allantois in size, so also in the Rodentia, *e. g.* rabbits and squirrels, the yelk-sac continues comparatively large during the whole period of pregnancy and the allantois small. In both groups the same course of development may be recognized, except that by the fusion of the allantochorion with the uterine mucous membrane, that is to say by the formation of a discoidal placenta, the function of the allantois is greatly increased. But the original conditions of the phylogenetic history may be inferred from the volume of the yelk-sac equalling that of the allantois for a long time.

A disciform vascular area with a cordifugal *sinus terminalis* upon the yelk-sac appears in perfectly homologous development in Marsupials, rabbits, and squirrels. The long persistence of an ecto-entodermal proamnion, which in the opossum is retained until birth, is likewise demonstrable in the above-mentioned Rodents. The inversion of the germinal layers in the Muridæ and Subungulata is to be regarded as a modification of a certainly very simple ancestral uterine development.

When considered from the phylogenetic standpoint all the organs of the Rodentia show themselves to be directly derivable from the type of the Marsupialia, and without any logical difficulty we may recognize step by step in the existing forms the stages which render the transformation of long-inherited arrangements intelligible. This fact has not struck me alone; it has forced itself directly upon every naturalist who has studied the different organs of the Rodents from the point of view of comparative anatomy, and I can only lay claim to the merit of having tested the correctness of the various scattered statements and combined them into a simple theory.

In the present report I have only expressed my views as to the phylogeny of the Rodentia without referring to other Mammalia. But I would not thereby convey the impression that I have occupied myself with that group alone; on the contrary, I have also taken other divisions into the range of my investigations, and have been led, with regard to the Insectivora and Bats, to the conclusion that between these two groups and the Marsupialia with Carnivoroid dentition there exists a very intimate relationship, which may be confirmed both anatomically and embryologically. Upon this subject, as upon the phylogeny of the Carnivora, I shall venture hereafter to report to the Academy.